EARLY DEVELOPMENT OF THE RAZORBACK SUCKER, $XYRAUCHEN\ TEXANUS\ (ABBOTT)$

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ABSTRACT.— Fertilized ova of razorback sucker, *Xyrauchen texanus*, were adhesive for 3 to 4 hours after fertilization. Cleavage was completed at 24 hours, gastrulation occurred at 34 hours, and blood circulation was established at 117 hours. Hatching occurred from 5.2 to 5.5 days after fertilization. Larvae were from 6.8 to 7.3 mm TL at hatching. Yolk was assimilated at 13 days (10 mm TL). All fins were formed and had ossified rays at 64 days (27 mm TL). The unique nuchal keel appeared about 200 days after fertilization.

The razorback sucker, Xyrauchen texanus (Abbott), is endemic to the Colorado River basin. As with much of the southwestern ichthyofauna (Pister 1981), it is declining in abundance (Minckley 1983). A program was commenced in 1974 to develop means of propagating the species (Toney 1974) and to delineate certain aspects of its life history. We studied embryological, larval, and juvenile development of the species in 1974-75. Although our data are somewhat outdated in light of recent studies of catostomid larvae (reviewed by Fuiman and Witman 1979), almost nothing has appeared on the early life history of this unique species. Winn and Miller (1954) presented a key to postlarval fishes of the lower Colorado River basin that included photographs and some descriptions of young X. texanus. A photograph by Douglas (1952: Fig. 3) was reidentified by Winn and Miller as speckled dace (Rhinichthys osculus [Girard]) rather than X. texanus. The present paper thus describes and figures early life-history stages of the razorback sucker as determined from hatchery-and laboratory-reared individuals.

METHODS

Initial information on hatchery propagation and rearing of razorback suckers originated from adult fish seined near Cottonwood Cove in Lake Mohave, Arizona-Nevada, in winter 1974, and was compiled by personnel at Willow Beach National Fish Hatchery (in part, Toney 1974). Eggs were stripped from females and fertilized, and developing young were initially housed in an indoor raceway at a mean water temperature of 14 C, then transferred 13 days posthatching to an outdoor raceway where water temperature averaged 15 C. Samples were preserved daily in 10 percent formalin during the first month, and intermittently thereafter. Late postlarval and juvenile phases described below are based on the 1974 cohort.

Additional adults were trammel netted from below Hoover Dam and in the vicinity of Carp Cove in Lake Mohave in March-April 1975. Most males were in active spawning condition, but females were either spent or not yet mature. Suitable females were interperitonealy injected with human chorionic gonadotropin, which induced oocyte maturation. A few hours after injection about 5,000 eggs were stripped from a single female and immediately fertilized with sperm of two males, as has been observed in nature (Douglas 1952). It is notable that water-hardened eggs obtained from naturally-matured females in 1974 were 2.9 mm diameter, but comparable ova obtained from hormone-induced maturation were 1.8 mm diameter. This disparity is far greater than has before been recorded in catostomid ova diameters (Fuiman and Trojnar 1980). We assume it resulted from precipitous maturation after hormone injection, but have no

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further explanation. By the time of hatching, both sets of embryos were of comparable length.

Developing embryos were maintained in an indoor raceway at Willow Beach for 28 hours at temperatures ranging from 13 to 17 C. Eggs were then transported to aquaria at Arizona State University, where development continued at a constant temperature of 20 C. Observations and measurements were recorded from living specimens by a stereomicroscope equipped with ocular micrometer and camera lucida, and with a range of magnification of 2 to 2,000 X. All measurements are of total length.

Observations on the 1975 cohort were made hourly through the first 30 hours, then every 2 hours until after hatching. Illustrations of selected stages through prolarval development were prepared through use of a camera lucida and from photographs. Ovum through prolarval development presented here is thus based on the 1975 fish. Specimens were preserved periodically in acetoformalic acid (AFA; 9.0 parts ethanol, 0.4 parts 40 percent formaldehyde, and 0.5 parts glacial acetic acid). When larvae began to swim and feed actively, samples were preserved less frequently.

Development of the razorback sucker was divided into four major phases as defined by Hubbs (1943): (1) embryological development, fertilization of the egg until hatching; (2) prolarval development, hatching to absorption of yolk; (3) postlarval development, yolk absorption to ossification of pelvic fin-rays; and, (4) juvenile development, pelvic ray ossification to maturation of gonads. Development staging followed Balinsky's (1948) general pattern for cyprinid fishes. Descriptive terminology was derived from Ryder (1885), Stewart (1926), Tavolga (1949), Winn and Miller (1954), and Long and Ballard (1976).

RESULTS

Embryological Development

Stage 1: unfertilized egg; day 0, 0 hour, 1.5 mm diameter. Ova milky white and translucent.

Stage 2: fertilized egg; day 1, 1 hour, 1.8 mm diameter. Chorion transparent and yolk milky-white and translucent; animal pole not yet visible to unaided eye. Water-hardened eggs with greater specific gravity than water, ova demersal, chorion adhesive, ova adhering to substrate and one another.

Stage 3: 2 blastomeres, 3 hours (Fig. 1A); beginning of cleavage. Blastomeres transparent, approximately 0.5 mm total diameter. Animal and vegetal poles distinguishable to unaided eye; ova telolecithal, cleavage meroblastic. Ova no longer adhesive. AFA preservation causes animal cells to whiten and become opaque; yolk becomes yellow white; chorion remains transparent.

Stage 4: 4 blastomeres, 5 hours; second cleavage. Blastomeres approximately 1.0 mm total diameter.

Stage 5: 8 blastomeres, 6 hours; third cleavage. Blastomeres occupy 1.2- by 0.8-mm rectangle on animal pole.

Stage 6: 16 blastomeres, 7 hours; fourth cleavage.

Stage 7: 32 blastomeres, 9 hours; fifth cleavage (Fig. 1B).

Stage 8: 64 blastomeres, 10 hours; sixth cleavage. 128 blastomeres, 11 hours; seventh cleavage. Large-celled blastula (morula); no blastocoel. Blastomeres occupy 25 percent of yolk surface.

Stage 9: small-celled blastula (morula), 14 hours. Individual cells distinguishable; blastomeres bulging upward from round yolk mass, occupying 25 percent of yolk surface. Blastomere layers progressively thinner toward periphery of blastoderm; no blastocoel.

Stage 10: morula, 24 hours (Fig. 1C). Individual cells indistinguishable except with high power and chorion removed; blastoderm with granular appearance; undersurface flat, lying on flattened surface of yolk sphere; no blastocoel. Cleavage terminated.

Stage 11: blastula (epiboly of blastoderm), day 2, 28 hours; 1.8 mm diameter (Fig. 1D). Blastoderm spreading over yolk sphere and thinning (blastodisc). Blastocoel present. Periblast visible as cellular rim along periphery of blastoderm, beginning formation of inner layer of yolk sac. Outer layer of yolk sac to be formed from epiblast derived from blastoderm. Blastoderm no longer bulging from yolk, capping under 33 percent of sphere.

Stage 12: early gastrula, 34 hours (Fig. 1E). Underrim of blastodisc thickened to form-"randwulst" or marginal ridge with inner layer termed the germ ring. Ring thickest posteriorly, recognized as embryonic shield. Presumptive endodermal cells at posterior edge of shield beginning to involute through blastopore and spread beneath blastoderm. Cells of prechordal plate and notochord migrating inward over dorsal lip of blastopore (establishment of embryonic axis). Presumptive mesodermal cells also turning inward, positioned either side of embryonic axis beneath ectoderm and above endoderm. Periblast, randwulst cells, and germ ring cells not involved in involution spread over 50 percent of yolk sphere.

Stage 13: middle gastrula, 35 hours. Invagination lengthening embryonic shield; blastopore marks posterior axis of embryo.

Stage 14: late gastrula, 36 hours (Fig. 1F). Embryonic shield nearly reaching animal pole of egg on dorsal meridian; shield approximately 1.3 mm long; concentration of invaginated cells clearly visible at anterior end of shield; randwulst cells and germ ring cells, accompanied by presumptive ectodermal cells, forming outwardly as epiblast; marginal ridge shifted below equator of egg; uncovered portion of yolk protrudes as yolk plug.

Stage 15: early neurula, 45 hours, 1.8 mm diameter. Blastopore closed; yolk plug no longer protruding. Embryonic shield approximately 2.0 mm long, circumscribing 75 percent of egg, overlying yolk sac. Neural plate formed, lateral and anterior margins not clearly delimited. Notochord in form of ridge pressing into yolk, lateral notochord rudiment not clearly separated from sheets of mesoderm.

Stage 16: late neurula, 47 hours (Fig. 1G). Neural keel remains 2.0 mm long, circumscribing 75 percent of egg. Neural plate contracted, more defined along edges. Cephalic region arrow shaped in dorsal view; eye rudiments forming; neural ridges as folds on either side of neural plate. Notochord separated from mesoderm.

Stage 17: eye rudiments, day 3, 49 hours, embryo length 2.0 mm. Brain cavities and spinal cord formed by contraction of neural plate. Eye rudiments as lateral protrusions at

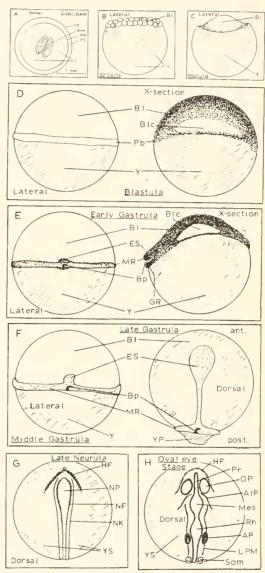


Fig. 1. Early embryological stages of razorback sucker, *Xyrauchen texanus*; chorion removed in all but A. Legend: AIP = anterior intestinal portal, Ant. = anterior, AP = auditory placode, BI = blastoderm, Blc = blastocoel, Blm = blastomere, Bp = blastopore, Ch = chorion, ES = embryonic shield, GR = germ ring, HF = head fold, LPM = lateral plate mesoderm, Mes = mesencephalon, MR = marginal ridge, NF = neural fold, NK = neural keel, NP = neural plate, OP = optic placode, Pb = periblast, PM = perivitelline membrane, PS = perivitelline space, Rh = rhombencephalon, som = somites, Y = yolk plug, and YS = yolk sac.

anterior end of brain. Prosencephalon (forebrain), mesencephalon (midbrain) and rhombencephalon (hindbrain) distinguishable. Audi-

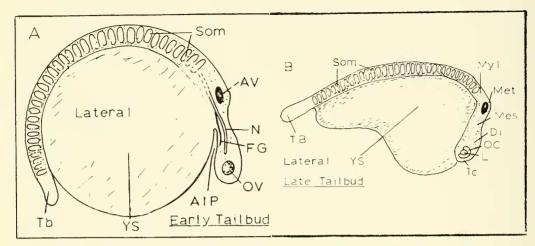


Fig. 2. Early (A) and late (B) tailbud embryological stages of razorback sucker, *Xyrauchen texanus*; chorion removed—embryo extended in "B." Legend as in Figure 1 when applicable, and AV = auditory vesicle, Di = diencephalon, FG = foregut, L = lens, Met = metencephalon, Myl = myelencephalon, N = notochord, OC = optic cup, OV = optic vesicle, TB = tailbud, and Te = telencephalon.

tory vesicles at level of hindbrain; first pair of somites present.

Stage 18: cavities in eye rudiments, 53 hours. Optic placodes elongated, containing narrow vesicles; head-fold visible; subcephalic pocket and anterior intestinal portal ventral to head. Auditory placodes formed; 14–16 pairs of somites.

Stage 19: oval eyes, 57 hours, 2.5 mm (Fig. 1H). Optic placodes rounded to oval; vesicles not yet present in auditory placodes; 30 pairs of somites. Tail process distinguishable.

Stage 20: early tailbud, 65 hours, 3.0 mm (Fig. 2A). Optic vesicles flattened on outer margins; lens forming. Auditory placodes with small vesicles. Tailbud developed, protruding from yolk sphere. Foregut forming.

Stage 21: late tailbud, day 4, 78 hours, 3.8 mm (Fig. 2B). Anterior portion of embryo (head and anterior trunk) overlying yolk sphere; posterior portion (posterior trunk and tail) overlying cylindrical yolk mass. Optic stalks, cups, and lenses distinguishable. Prosencephalon divided into telencephalon (future cerebrum) and diencephalon (future epithalamus, thalamus, and hypothalamus); rhombencephalon divided into metencephalon (future cerebellum) and myelencephalon (medulla oblongata). Heart rudiment present; tailbud lengthening, embryo motile within chorion.

Stage 22: heart beat, 83 hours, 4.0 mm. Heart pulsations noted. Tail at right angle to

body axis. Kidney ducts (pronephric ducts) and dorsal aorta formed ventral to neural tube and notochord; alimentary tract lined by endoderm and nearly complete; stomadeum and proctodeum not apparent.

Stage 23: fin fold, day 5, 103 hours, 5.3 mm. Fin fold appearing on tail and posterior dorsum; head growing outward from yolk sac. Circulatory system formed; nasal placodes present; tail beginning to straighten.

Stage 24: blood circulation, 117 hours, 6.8 mm (Fig. 3). Head extending from yolk. Heart visible within pericardial cavity; flexed, sinus venosus and atrium lying above and left of ventricle and conus arteriosis; endocardium and epimyocardium distinguishable. Three visceral (gill) arches formed; pupils visible within eyes, brown pigment granules in choroid regions. Yolk reduced to cylinder below body axis. Blood flow: atrium → ventricle → conus arteriosus → ventral aorta → branchial afferents → branchial efferents → dorsal aorta and internal carotid arteries → vitelline artery → caudal vein → posterior cardinal vein → anterior cardinal and vitelline veins → common cardinal vein (Duct of Cuvier) → sinus venosus → atrium. Embryos extremely motile, some beginning to rupture chorion.

Stage 25: pectoral fin rudiments, 120 hours, 6.8 mm. Pectoral fin anlagen appearing posteriad and ventrad to auditory vesicles. Tail slightly upturned. Stomadeum

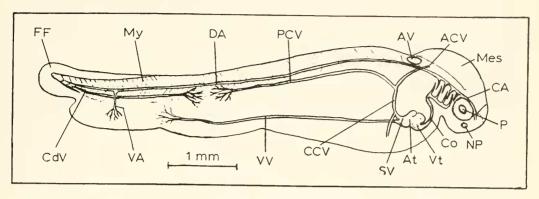


Fig. 3. Embryo of razorback sucker, *Xyrauchen texanus*, at initial circulation of blood; embryo extended and chorion not depicted. Legend as in Figures 1 and 2 when applicable, and ACV = anterior cardinal vein, At = atrium, CA = carotid artery, CCV = common cardinal vein (duct of Cuvier), CdV = caudal vein, Co = conus artriosus, DA = dorsal artery, FF = fin fold, My = myomeres, NP = nasal placode, P = pupil, PCV = posterior cardinal vein, SV = sinus venosus, VA = vitelline artery, Vt = ventricle, and VV = ventral vein.

clearly visible. Myotomes discernible above yolk. Embryos flex once every 12 to 13 heart beats.

Stage 26: pectoral fin buds, day 6, 125 hours, 7.3 mm. Rudiments of pectoral fins protrude, slightly flattened dorso-ventrally. Head continuing to extend outward from yolk.

Prolarval Development

Stage 27: hatching, 131 hours, 7.3 mm (Fig. 4). Pectoral fin buds paddle shaped. Tail straightened and median fin fold developed anteriorly on dorsum. Head flexed 45 degrees relative to body axis. Proctodeum discernible; eye pigment increased. Embryos scarcely motile, flexing along bottom with no directed movements.

Stage 28: 142 hours, 7.5 mm. Four gill arches visible; head remains at 45 degree angle to body axis. Pectoral fin buds thin and

broadly rounded; ventral fin fold appearing behind proctodeum.

Stage 29: 144 hours, 7.5 mm. Lower jaw formed, not yet reaching level of eye; mouth oriface round. Head angle less than 45 degrees relative to body axis.

Stage 30: early prolarva, day 7, 162 hours, 8.0 mm (Fig. 5). Head straightened. Lower jaw reaching midlevel of eye, not movable. Pectoral fin differentiated into muscular lobe and membrane, not movable. Ventral fin fold developed to most anterior extension, embryonic fin membrane (continuous median fin) complete. Opercular membranes forming. Optic pigmentation brown, granular, almost complete; no other melanophores.

Stage 31: middle prolarva, day 9, 238 hours, 9.0 mm. Rudimentary gas bladder evident. Lower jaw to anterior border of eye, movable; mouth rounded and terminal. Opercle covers anteriormost gill. Pectoral fin 0.5 mm long, movable. Proctodeum yet

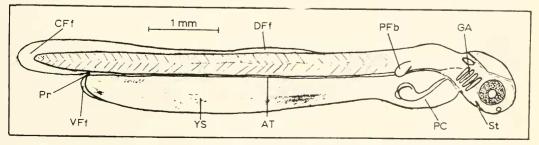


Fig. 4. Prolarva of razorback sucker, *Xyrauchen texanus*, at hatching; legend as in Figures 1 to 3 when applicable, and AT = alimentary tract, CFf = caudal fin-fold, DFf = dorsal fin-fold, GA = gill arches, PC = pericardial cavity, PFb = pectoral fin-bud, Pr = proctodeum, St = stomadeum, and VFf = ventral fin-fold.

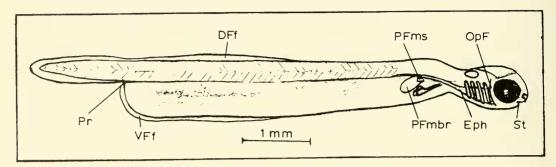


Fig. 5. Early prolarva of razorback sucker, *Xyrauchen texanus*; legend as in Figures 1 to 4 when applicable, and Eph = esophagus, OpF = opercular flap, Pfmbr = pectoral fin membrane, and PFms = pectoral fin musculature.

closed, yolk much reduced. Eye pigmentation completed, becoming black. Brown, stellate melanophores on ectoderm overlying midand hindbrain, and on paired dorsal pigment line, paired dorso-visceral pigment line (upper body cavity), and unpaired midventral pigment line. No melanophores on horizontal myoseptum. Larvae swim to surface and feed on ground aquarium fishfood (Tetramin^R). Resting heart rate 120 beats per minute.

Stage 32: late prolarva, day 10, 263 hours, 9.0 mm (Fig. 6). Liver reaching midventral line; yolk largely assimilated. Pectoral fins 0.8 mm long, no fin rays in any fin. Pigmentation increasing on dorsal, dorso-visceral, and midventral lines; melanophores on lateral pigment line, opercle, and at pectoral fin base.

Postlarval Development

Stages 33 and 34: assimilation of yolk, day 12, 311 hours, 10.0 mm. Yolk assimilated, proctodeum open to form anus. Opercles cover two anteriormost gills. Otoliths present in auditory vesicles. Pectoral fins with 3 rays;

caudal fin with 3 or 4 rays; no trace of dorsal or anal fins. Spleen forming posterior to liver. Posterior end of notochord (urostyle) upcurved. Pigmentation increased on all aspects except lateral pigment line; melanophores appearing on gas bladder.

Stage 35: early postlarva, day 17, 430 hours, 12.0 mm. Caudal fin-rays increased to 7 to 9. Opercles cover gills. Median fin fold thickened and expanded at sites of anal and dorsal fins. Food materials in stomach; feces passing through intestine. All pigmentation excepting lateral pigment line intensified.

Stage 36: dorsal and anal fin-ray rudiments, day 40, 960 hours, 15.5 mm (Fig. 7). Fin-ray rudiments in dorsal and anal fins; caudal fin with full complement of ossified rays. Gas bladder constricting into two chambers. Melanophores appearing on posterior part of lateral pigment line.

Stage 37: middle postlarva, day 48, 1152 hours, 20.0 mm. Rays of dorsal and anal fins partially ossified; pelvic fins rudimentary as gatherings of mesenchyme; caudal fin becoming emarginate. Gas bladder two chambered. Urogenital papilla apparent. Mouth terminal;

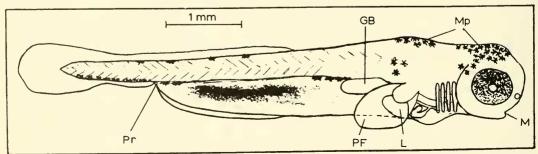


Fig. 6. Late prolarva of razorback sucker, $Xyrauchen\ texanus$; legend as in Figures 1 to 5 when applicable, and GB = gas bladder, L = liver, M = mouth, Mp = melanophores, and PF = pectoral fin.

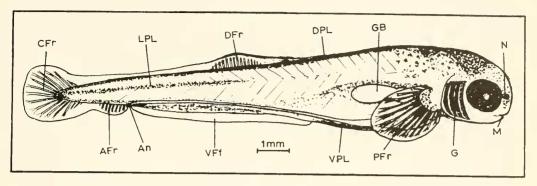


Fig. 7. Postlarva of razorback sucker, $Xyauchen\ texanus$, at beginning of fin-ray development; legend as in Figures 1 to 6 when applicable, and AFr = anal fin-rays, An = anus, CFr = caudal fin-rays, DFr = dorsal fin-rays, DPL = dorsal pigment line, G = gills, LPL = lateral pigment line, N = naris, PFr = pectoral fin-rays, and VPL = ventral pigment line.

lips formed, small papillae on both upper and lower lips. Melanophores increasing over body; ossified fin rays and gills acquiring pigment; larvae dark dorsally and lighter ventrally and in eye region.

Stage 38: pelvic fin rudiments, day 50, 1200 hours, 20.8 mm. Pelvic fin rudiments in form of small crescentic folds.

Stage 39: pelvic fin buds, day 54, 1296 hours, 23.5 mm. Pelvic fin buds in form of thin membranous paddles, not movable.

Stage 40: pelvic fin rudiments, day 64, 1536 hours, 27.0 mm. Six pelvic fin-ray rudiments within pelvic fin membranes; fin movable. Dorsal and anal fin-rays completely ossified. Mouth beginning to shift ventrally, papillae highly developed on lips.

Stage 41: ossification of pelvic fin-rays, day 70, 1680 hours, 32 mm. Rays partially ossified in pelvic fins; median fin membrane persisting ventrally and anterior to pelvic fins greatly reduced; dorsal and anal fins separated from caudal fin.

Stage 42: late postlarva, day 75, 1800 hours, 35 mm (Fig. 8). Pelvic fin-rays ossified. Median fin membrane persisting only between anus and pelvic fins. Full complements of fin-rays in all fins: dorsal, 15-16; caudal, 19; anal, 8; pelvic, 9-9; and pectoral, 13-15-13-15. Narial flap formed. Alimentary tract looped once to left just posterior to stomach, mouth ventral. Acoustico-lateralis system formed on anterior half of body.

Juvenile Development

Stage 43: scale rudiments, day 105, 2520 hours, 43.0 mm. Scale rudiments present on ventro-lateral surfaces; median fin membrane eliminated.

Stage 44: scales, day 125, 3000 hours, 45.0 mm. Scales distinctly visible except medially on dorsum and ventrum.

Stage 45: nuchal keel, day 227, 5448 hours, 90.0 mm (Fig. 9). Scalation completed. Acoustico-lateralis system completed. Nuchal

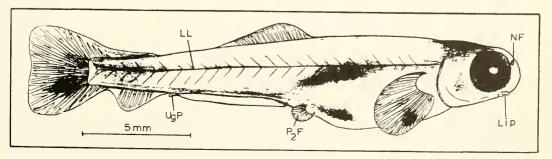


Fig. 8. Late postlarva of razorback sucker, $Xyrauchen\ texanus$; legend: LL = lateral line, Lip = papillose lips, NF = nasal flap, P_2F = pelvic fin, and UgP = urogenital papillus.

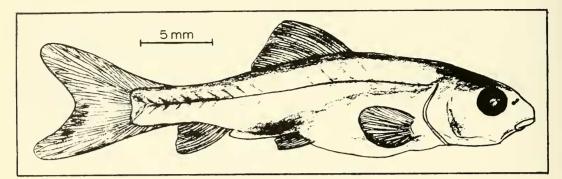


Fig. 9. Juvenile of razorback sucker, Xyrauchen texanus, shortly after initiation of nuchal keel.

keel evident to touch on predorsum. Except for further development of nuchal keel, evident to the eye at a 250–300 days of age (Fig. 10), morphogenesis is completed. Individuals from the 1974 cohort achieved sexual maturity in their sixth year of life (Minckley 1983).

SUMMARY

Fertilized, water-hardened ova of *Xyrau-chen texanus* were 1.8 mm in diameter from females hormone-induced to mature and 2.9 mm from females that matured naturally.

Eggs were adhesive for 3 to 4 hours after fertilization. Cleavage was completed in 24 hours at temperatures varying from 13 to 17 C; further development was at 20 C. Gastrulation occurred at 34 hours. The notocord separated from the mesoderm at 47 hours, and eye rudiments and brain cavities were distinguishable at 49 hours. The tail process formed at 57 hours (2.5 mm). Heart beat began at 83 hours, and blood circulation was established at 117 hours. Embryos began vio-

lent flexing and some ruptured their chorions at that time. All hatched between 125 and 131 hours after fertilization.

Embryos were 6.8 to 7.3 mm TL at hatching. The yolk sac is tubular, and the head flexes over it at a 45 degree angle to the body axis. The pectoral fin buds, noted at 120 hours (6.8 mm), became paddlelike at 162 hours (8.0 mm), and first were movable at 238 hours (9.0 mm). The continuous, median fin fold first noted on caudal and posterodorsal areas at 103 hours (5.3 mm), began to develop on the venter (behind the proctodeum) at 142 hours (7.5 mm), and was continuous at 162 hours (8.0 mm). The opercles began forming at 162 hours (8.0 mm). The gas bladder first appeared at 238 hours (9.0 mm). The lower jaw became movable and prolarvae began directed swimming to the sur face to feed at that time; eye pigment complete and black. Melanophores developed over mid- and hindbrain and on paired dorsal, paired dorso-visceral, and unpaired midventral pigment lines between 162 and 238 hours (8.0 and 9.0 mm). There was no lateral

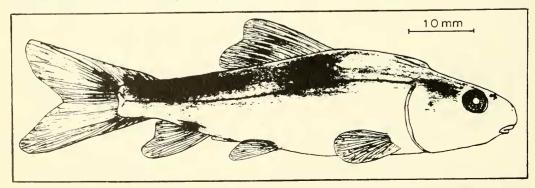


Fig. 10. Juvenile of razorback sucker, Xyrauchen texanus, with essentially adult morphology.

pigmentation at 9.0 mm. Melanophores on the dorsum are large and stellate, as also recorded by Winn and Miller (1952). At 263 hours (9.0+ mm) fin rays were not yet visible in any fin.

Yolk was completely assimilated at 311 hours (10.0 mm) and the proctodeum opened to form the anus. The urostyle became upturned between 263 and 311 hours, and 3 to 4, ventral, caudal fin-rays formed by the last time period. Pectoral fins had developed three rays, but there were no rays in the dorsal and anal fins. Median fin folds were thickened and expanded at the sites of the future dorsal and anal fins at 430 hours (12.0+ mm), and the opercles fully covered the gills. Dorsal and anal fin-ray rudiments, and a lateral pigment line appeared at 960 hours (15.5 mm). The gas bladder had by this time constricted toward the two-chambered condition. Pelvic fins appear as swellings of mesenchyme and the caudal fin becomes emarginate at 1152 hours (20.0 mm). The pelvic fin buds were nonmovable, membraneous paddles at 1296 hours (23.5 mm); movement and pelvic fin-rays had appeared at 1536 hours (27.0 mm).

Scale rudiments were first noted at 2520 hours (43.0 mm) on ventrolateral body surfaces. By 3000 hours, lepidogenesis was complete on all but the median areas of the dorsum and ventrum. The nuchal keel appeared about 5000 hours after fertilization.

ACKNOWLEDGMENTS

This research was supported, in part, by U.S. Fish and Wildlife Service Contract 14-16-0002-3585 to Arizona State University. We thank personnel at Willow Beach National Fish Hatchery for assistance in obtain-

ing and rearing young of razorback suckers. Permits for collection of wild fish were granted by Arizona Game and Fish Department. J. P. Collins and R. W. McGaughey read and commented on the manuscript.

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